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Identification of additional sources of resistance to *Puccinia striiformis* f. sp. *hordei* (PSH) in a collection of barley genotypes adapted to the high input condition

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Abstract

A total of 336 barley genotypes consisting of released cultivars, advanced lines, differentials and local landraces from the ICARDA barley breeding programme were screened for seedling and adult-plant resistances to barley stripe rust pathogen (*Puccinia striiformis* f. sp. *hordei* [PSH]). Seedling resistance tests were undertaken at Shimla, India by inoculating 336 barley genotypes with five prevalent PSH races [Q (5S0), 24 (0S0-1), 57 (0S0), M (1S0) and G (4S0)] in India. Barley genotypes were also evaluated at the adult-plant stage for stripe rust resistance at Durgapura (Rajasthan, India) in 2013 and 2014, and at Karnal (Haryana, India) in 2014 under artificial PSH infection in fields, using a mixture of the five races. Twelve barley genotypes (ARAMIR/COSSACK, Astrix, C8806, C9430, CLE 202, Gold, Gull, Isaria, Lechtaler, Piroline, Stirling, and Trumpf) were resistant to all five PSH races at the seedling and adult-plant stages. Two of these genotypes, Astrix and Trumpf, were part of international differentials and reveal that five races were avirulent to genes *Rps4* (*yr4*), *rpsAst*, *rpsTr1* and *rpsTr2*. These genes were highly effective against PSH races prevalent in India. The virulence/avirulence formula reported in this study helped to determine the effectiveness of PSH resistance genes against Indian races. Forty-five genotypes showed adult-stage plant resistance (APR) in the field. The identified PSH resistant genotypes may possess novel resistance genes and might serve as potential donors of PSH resistance at seedling and APR in the future. Further research is needed to determine the nature of resistance genes through allelic studies and mapping of these genes.

KEYWORDS
barley, hordeum, *Puccinia*, race, resistance, stripe rust, yellow rust

1 | INTRODUCTION

Stripe rust of barley (*Puccinia striiformis* Westend. f. sp. *hordei* Eriks.) (PSH) occurs worldwide. Currently, it is one of the major fungal diseases of barley in various parts of South Asia (Bahl & Bakshi, 1963; Bakshi, Bahl, & Kohli, 1964; Luthra & Chopra, 1990; Murty, 1942; Vaish, Ahmed, & Prakash, 2011), South America and North America (Chen, Line, & Leung, 1995; Dubin & Stubbs, 1986; Roelfs & Huerta-Espino, 1994) and Eastern Africa (Woldeab, Fininsa, Singh, & Yuen, 2007). Specifically, in the hills of India, stripe rust is a major biotic

factor limiting barley production. Vaish et al. (2011) reported stripe rust as the most destructive disease resulting in 66% yield loss on susceptible cultivars in the trans-Himalayan region of India. Among various disease management options, stripe rust can be managed effectively by the use of fungicides; however, use of fungicides is not an economic and environmentally friendly option for barley farmers. Genetic resistance to stripe rust is the most effective, economic and environmentally viable option to manage the disease (Broers & Jacobs, 1989).

Several races were reported during 1940–1990 in India, which have overcome available resistance sources (Bahl & Bakshi, 1963; Bakshi et al., 1964; Luthra, 1966; Luthra & Chopra, 1990; Murty, 1942). The earliest genetic study on stripe rust in India was reported by Murty (1942) where two dominant resistant genes in "Alpha," an American cultivar, were reported. Several other early reports, on genetic studies from India, included characterization of PSH races prevalent in India and genes conditioning resistance to PSH. Identification of new and additional sources of resistance to stripe rust and understanding the genetic mechanisms/diversity underlying the resistance sources are, therefore, prerequisites for gene mapping, resistant cultivar development and their deployment in the field. Races 57 (0S0), 24 (0S0–1), G (4S0), M (1S0) and Q (5S0) were periodically characterized in India using Indian PSH differential set (Bahl & Bakshi, 1963; Bakshi et al., 1964; Luthra & Chopra, 1990). Several stripe rust resistance genes were reported by Indian researchers using Indian differential set challenged with PSH races while they used *Yr/yr* symbols for resistance gene designations (Bahl & Bakshi, 1963; Bakshi et al., 1964; Luthra & Chopra, 1990). Earlier, Johnson (1968) and Nover and Scholz (1969) reported *yr1*, *yr2*, *yr3* and *Yr4* genes in differential sets used in India. In addition to this, Luthra, Verma, and Prabhu (1991) reported that *Yr4* in EB 410; *yr5* in EB 438 and EB 1556; *yr6* in EB 1556; *yr7*, *yr8*, and *yr9* in EB 1626; *yr1*, *Yr10*, and *Yr11* in Abyssinian 14; and *yr3*, *Yr12*, and *Yr13* in I 5 were effective against PSH races existing in India. The use of *Yr/yr* symbol for PSH resistance gene(s) by Indian researcher is not consistent with international researchers. In contrast, Indian researchers frequently used PSH race 24 to characterize resistance gene in Indian germplasm (Bahl & Bakshi, 1963; Bakshi et al., 1964; Chen & Line, 2002; Chen et al., 1995; Johnson, 1968; Luthra & Chopra, 1990; Nover & Scholz, 1969). Therefore, resistance identified and characterized against race 24 was effective on a wider scale. After 1990, new PSH races were reported in India, which have overcome previously reported resistance in barley (Nayar, Prashar, & Bhardwaj, 1997; Prashar, Bhardwaj, Jain, & Datta, 2007). Vaish et al. (2011) found that stripe rust had the highest incidence on barely in the trans-Himalayan Ladakh region in India, suggesting previously reported resistance genes were not effective in recent years. Therefore, in addition to the Indian differential set, international PSH differential set is desirable to be used to characterize Indian PSH races more accurately and to determine the effectiveness of resistance genes against virulent PSH races prevalent in India. Recently, Gyawali et al. (2017) reported PSH resistance in barley (adapted to low input conditions) collection in ICARDA using Indian races. The PSH resistance of barley genotypes, (collected at ICARDA) adapted to high input conditions, against Indian races is still unknown. Hence, the objectives of this study were as follows: (1) to identify additional sources of resistance in the germplasm used by the ICARDA barley breeding programme for high input conditions against PSH races originating from India and (2) to determine the response of an international collection of barley genotypes and cultivars to commonly existing PSH races in India.

2 | MATERIALS AND METHODS

2.1 | *Barley genotypes and* Puccinia striiformis *f. sp.* hordei *races*

The 336 barley genotypes consisted of released cultivars, advanced lines, differentials, and local landraces, collected from diverse sources including the ICARDA's barley breeding programmes. Barley collection reported here includes genotypes that are adapted to high input condition. At ICARA, high input condition is defined as a favourable barley production condition with no moisture and nutrient stress. The passport data of 336 barley genotypes and their response to Indian PSH races at the seedling and adult-plant stage are presented in Table S1. Majority of barley genotypes were originated from various breeding programmes in North America, South America, Europe and Australia. Except for a few Indian genotypes included in this study, majority of barley genotypes was never tested for resistance to existing PSH races in India. Therefore, barley genotypes were evaluated for seedling resistance in the temperature-controlled glasshouse at ICAR-Indian Institute of Wheat and Barley Research (IIWand BR), Regional Station, Shimla, India, individually, against five PSH races, namely 57 (0S0), 24 (0S0–1), M (1S0), Q (5S0), and G (4S0) (Bahl & Bakshi, 1963; Bakshi et al., 1964; Luthra & Chopra, 1990). Among these races, 57, 24 and G were old races while Q and M were recently characterized races (Nayar et al., 1997; Prashar et al., 2007) in India. The lists of international and Indian barley stripe rust differential sets are presented in Table 1 along with stripe rust resistance genes present in individual barley genotypes.

Eleven barley genotypes (genotypes 2–12) (Table 1) used in new Indian differential set were common to the International differential set while five genotypes 16–20 were common to traditional (old) Indian differential set. Among the genotypes of traditional Indian differential set that was used in this study, the gene(s) possessed by Alfa 93 (Quilmes Alfa), Fong Tien, and Dolma are unknown. Therefore, barley genotypes EB410, EB438, EB1556 and EB1626, with known gene(s) resistance to PSH races in India, were included in Indian differential set to develop a virulence/avirulence formula which is important to resistance breeding programmes in the future. PSH races have been characterized using Indian differential genotypes of barley at ICAR-IIWand BR Regional Station, Shimla (Nayar et al., 1997). In brief, for the purpose of nomenclature, a system based on binary notation was proposed by Nagarajan, Nayar, and Bahadur (1983), modified subsequently (Prashar et al., 2007) was used. In India, this system has been used for barley stripe rust pathotyping since 1983.

TABLE 1 Barley genotypes used to differentiate infection types of *Puccinia striiformis* f. sp. *hordei* races

North American differentials[a]			Indian differentials[b]		
No.	**Differential genotype[c]**	**Gene(s)[d]**	**No.**	**Differential genotype[c]**	**Gene(s)[d]**
1	Topper	No known genes	1	EB 410[e]	*Ps1*
2	Heils Franken	*Rps4* (***Yr4***), *rpsHF*	2	Heils Franken	*Rps4* **(*Yr4*)**, *rpsHF*
3	Emir	*rpsEm1*, *rpsEm2*	3	Emir	*rpsEM1*, *rpsEm2*
4	Astrix	*Rps4* (***Yr4***), *rpsAst*	4	Astrix	*Rps4* **(*Yr4*)**, *rpsAst*
5	Hiproly	*rpsHi1*, *rpsHi2*	5	Hiproly	*rpsHi1*, *rpsHi2*
6	Varunda	*rpsVa1*, *rpsVa2*	6	Varunda	*rpsVa1*, *rpsVa2*
7	Abed Binder 12	*rps2* (***yr2***)	7	Abed Binder 12	*rps2* **(*yr2*)**
8	Trumpf	*rpsTr1*, *rpsTr2*	8	Trumpf	*rpsTr1*, *rpsTr2*
9	Mazurka	*rps1.c*	9	Mazurka	*rps1.c*
10	Bigo	*rps1.b* (***yr***)	10	Bigo	*rps1.b* **(*yr*)**
11	I 5	*rps3* (***yr3***), *rpsI5*	11	I 5	*rps3* (***yr3***), *rpsI5* **(*Yr12*, *Yr13*)**
12	Abyssinian 14	*rpsA14-1*, *RpsA14-2*	12	Abyssinian 14	*rpsA14-1*, *RpsA14-2* **(*yr1*, *yr10*, *yr11*)**
13	BBA 2890	*rps1.a*	13	EB438[e]	*ps4*
14	BBA 809	*rpsBBA809*	14	EB1556[e]	*yrEB15561*, *ps4*
15	Cambrinus	*Rps4* (***Yr4***)	15	EB1626[e]	*yrEB1626-1*, *yrEB1626-2*, *yrEB1626-3*
16	Grannelose Zweizeilige	*rpsGZ*	16	Fong Tien	*Susceptible check*
17	PI 548708	*rpsPI548708-1*, *rpsPI548708-1*	17	Himani[e]	*Ps1*, *ps4*
18	PI 548734	*rps1.a*, *rpsPI548734*	18	Alfa93 (Quilmes Alfa)	*Unknown*
19	PI 548747	*rpsPI548747-1*, *rpsPI548747-1*	19	Dolma	*Unknown*
20	Stauffers Obersulzer	*rpsSO-1*, *rpsSO-2*	20	Bilara-2	*Susceptible check*

[a]North American differential set and gene symbols were adapted from Line (2002).
[b]Genotypes used as stripe rust differential set in the study at Indian Institute of Wheat and Barley Research (IIW&BR), Regional Station, Shimla, India.
[c]Differential genotypes used for the stripe rust resistance. Differential genotype # 1–12 of international set were tested in this study.
[d]Gene symbols in parenthesis (boldface italicized letter) as designated by Indian Scientists.
[e]Gene symbol for the genotype was designated according to Luthra and Chopra (1990).

The constituents of this differential set have been placed in three groups which are named as "Set-0," "Set-A" and "Set-B" (Nayar et al., 1997). The stripe rust races are being maintained in pure and virulent forms on susceptible barley cultivar "Bilara-2" at the station using the single spore culture method.

2.2 | Screening for seedling resistance

Seedling resistance of 336 barley genotypes to individual races (57, 24, G, M and Q) was evaluated at ICAR-IIWand BR, Regional Station, Shimla, India. Aluminium bread pan trays of size 29 cm long × 12 cm wide × 7 cm deep, filled with a mixture of fine loam and farmyard manure (3:1), were used for growing seedlings. Twenty holes (10 holes in each row, 4 cm deep and 5 cm apart) were made with the help of wooden marker in the soil bed. About 4–5 seeds were sown in each hole representing one genotype. Total 18 test genotypes were accommodated in each tray. In addition, "Bilara-2" (susceptible check) was planted always at of seventh and 14th holes in the tray. The seedlings were raised in spore-proof glasshouse chambers at 22 ± 2°C, 50%–70% relative humidity, and 12-hr daylight cycle. One-week-old seedling with fully expanded primary leaves was inoculated using a glass atomizer that contained 100 mg spores of individual race suspended in 10 ml light grade mineral oil (Soltrol 170, Chevron Phillips Chemicals Asia Pvt. Ltd., Singapore). The plants were sprayed with a fine mist of sterile water and placed for 48 hr in dew chambers at 16 ± 2°C with >90% relative humidity and 12-hr day/night cycle. The plants were then transferred to glasshouse tables and incubated at 16 ± 2°C with >70% relative humidity, illuminated at about 15,000 lux for 12 hr. Fine elemental sulphur was dusted on the plants immediately after taking them out of the dew chambers. Being wet, elemental sulphur dust got deposited on the leaves and prevented any infection of powdery mildew, without affecting rust infections, sporulation and pustule development.

Infection types (ITs) (resistant and susceptible) on barley genotypes were recorded 16–18 days after inoculation using the modified method from Nayar et al. (1997) and Stakman, Stewart, and Loegering (1962). The ITs were characterized as 0; (naught fleck) = no visible infection; (Fleck minus) = slightly necrosis/micro-flecking visible; (Fleck) = no uredia but small hypersensitive flecks present, 1 (one) = uredia minute, surrounded by distinct necrotic areas, 2 (two) = small-to-medium uredia surrounded by chlorotic or necrotic border, 3 (three) = uredia small to medium in size and chlorotic areas may be present, 3+ (Three plus) = uredia large with or without chlorosis, sporulating profusely and forming rings. Infection type 33+ is classified when both 3 and 3+ pustules occur together. The experiment was repeated once to ascertain the consistency of the ITs. Infection types of 0–2 were considered resistant and ITs of 3 to 3+ as susceptible.

2.3 | Adult-plant stage resistance screening

The same set of 336 genotypes was screened in field under artificial inoculation conditions for adult-plant stage resistance to stripe rust at stripe rust hot spots: ARS, (RAU) Durgapura (75°47′E, 26°51′N), Rajasthan, India during 2012–2013; Durgapura, and at ICAR-IIWBR, Karnal (76°98′E, 29°69′N), Haryana, India during 2013–2014. The maximum and minimum monthly temperature and average relative humidity during inoculation and rust development are collected from meteorological stations located in each research stations (Table S2). The experiment was laid out in augmented design where the susceptible check, Bilara-2, was repeated in each block of 20 test genotypes. The same experimental design was used in 2013 and 2014 at both locations. One metre rows of each genotypes were planted with 25-cm row spacing in first fortnight of November each year at Durgapura and Karnal. Spreader rows of "Bilara-2" were also seeded perpendicular to the test plots throughout the experimental blocks as well as around the perimeter of the test blocks to ensure sufficient inoculum pressure and to avoid disease escape. To multiply the initial inoculum, one plot of six rows of Bilara-2 was seeded about 15 days before planting of the experimental material. The screening for stripe rust resistance was undertaken artificially using a mixture of the five races 57 (0S0), 24 (0S0–1), G (4S0), M (1S0) and Q (5S0) received from ICAR-IIWand BR Regional Station, Shimla. Prior to inoculation, the five races were mixed in equal amounts for inoculating the plants in spreader rows. The spreader plots were first syringe inoculated at 21-day-old seedling (Zadoks GS 20) with the mixed inoculum of stripe rust races followed by repeated sprays of inoculum collected from spreader rows on the test material. The field was given extra irrigations to maintain an appropriate humid microclimate for the better development of disease ensuring sufficient inoculum loads. Stripe rust severity was recorded at the early to late flowering stages (Zadoks GS 60–69) when maximum disease incidence was achieved.

A modified Cobb scale (Peterson, Campbell, & Hannah, 1948) was used in the field to assess stripe rust severity (percentage leaf area affected), and host responses were recorded as R = no uredia present; TR = trace or minute uredia on leaves without sporulation; TMR = trace or minute uredia on leaves with some sporulation; MR = small uredia with slight sporulation; MR–MS = small-to-medium-sized uredia with moderate sporulation; MS–S = medium-sized uredia with moderate to heavy sporulation; and S = large uredia with abundant sporulation, uredia often coalesced to form lesions as outlined by Roelfs, Singh, and Saari (1992). Disease severity and host responses were then combined to represent field response for each genotype.

The maximum disease score on the genotypes recorded over locations/years was taken into consideration to classify them into resistant, moderately resistant, moderately susceptible and highly susceptible categories. Genotypes were classified as resistant if no apparent symptoms or flecking on the leaf to traces of resistant-type pustules (using IT symbol). The ratings were considered moderately resistant if the plant had stripe rust severity up to 10MR over 2 years at two locations. Plants were recorded as moderately susceptible if plant had stripe rust severity 5S to 20MS highest reaction. More than 20MS score were considered as susceptible reaction. The MS and S reactions showed medium to well-developed rust pustules with no yellowing tissues around and more sporulation. The principal component analysis (PCA) was performed in R-program using princomp command for both seedling and adult-plant stage data.

3 | RESULTS

The two key research stations: ARS (RAU) Durgapura and ICAR-IIWand BR Karnal were used in the study. Durgapura is the key location where weather conditions (temperature and humidity) favour stripe rust development (Table S2) as compared to Karnal location, where severe winters sometimes do not support the faster development of the rust for secondary spread. The range of field reaction of stripe rust was higher at Durgapura as compared to Karnal in general; however, the reaction of Bilara-2 was always 100S at both the locations (Table S1).

Bilara-2 was susceptible at seedling stage to all five PSH races that were used in this study in the field. Alfa 93 (unknown) was resistant to all races except for race M (Table 2). Alfa 93 showed a moderately resistant reaction to race M. Hiproly (*rpsHi1*, *rpsHi2*) was effective against all races except 57, Abed Binder 12 (*rps2* [*yr2*]) was effective to all races except 24 and Dolma (unknown) was effective against all races except M. In contrast, Heilis Franken (*Rps4* [*Yr4*], *rpsHF*) was effective against only race G. Varunda (*rpsVa1*, *rpsVa2*) was effective against three races (Q, 57, and G) of five. Emir (*rpsEM1*, *rpsEm2*) was effective against races Q and 57 while Abyssinian 14 (*rpsA14-1*, *RpsA14-2* [*yr1*, *yr10*, *yr11*]) was effective against Q and M only. Mazurka (*rps1.c*) and Fong Tien (unknown) were susceptible to all races; Bigo (*rps1.b* [*yr*]) was susceptible to races M and G.

The effectiveness of stripe rust resistance gene(s) to each of the five races was described using virulence/avirulence formula

TABLE 2 Seedling reactions of barley differentials to different races of *Puccinia striiformis* f. sp. *hordei* at Indian Institute of Wheat and Barley Research, Shimla, India

		PSH races[a]				
Genotype	**Gene**	**57(0S0)**	**24(0S0–1)**	**G(4S0)**	**M(1S0)**	**Q(5S0)**
EB 410[b]	*Ps1*	0	0	0	0	0
Heils Franken	*Rps4* **(*Yr4*)**, *rpsHF*	3+	3	0	3+	3+
Emir	*rpsEM1*, *rpsEm2*	0	3+	3	3+	0
Astrix	*Rps4* **(*Yr4*)**, *rpsAst*	0	0	0	0	0
Hiproly	*rpsHi1*, *rpsHi2*	3+	0	–	–	–
Varunda	*rpsVa1*, *rpsVa2*	3	0	0	3+	2+
Abed Binder 12	*rps2* **(*yr2*)**	0	3+	0	0	0
Trumpf	*rpsTr1*, *rpsTr2*	0	0	0	0	–
Mazurka	*rps1.c*	3+	3+	3+	3+	3+
Bigo	*rps1.b* **(*yr*)**	3+	3+	0	0	3+
I 5	*rps3* (***yr3***), *rpsI5* **(*Yr12*, *Yr13*)**	3	3	3	3+	3
Abyssinian 14	*rpsA14-1*, *RpsA14-2* **(*yr1*, *yr10*, *yr11*)**	3	3+	3+	0	0
EB438[b]	*ps4*	0	0	0	0	0
EB155[b]	*yrEB1556-1*, *ps4*	0	0	0	0	0
EB1626[b]	*yrEB1626-1*, *yrEB1626-2*, *yrEB1626-3*	0	0	0	0	0
Fong Tien[b]	*Absent*	3+	3+	3+	3+	3+
Himani[b]	*Ps1*, *ps4*	0	0	0	0	0
Alfa93	*Unknown*	–	–	–	2+	0
Dolma	*Unknown*	–	0	–	3	0
Bilara-2[c]	*Absent*	3+	3+	3+	3+	3+

[a]The virulence pattern is based on Indian barley stripe rust differential set used in this study including EB401, EB438, EB155, EB1626, Fong Tien, Himani, Alfa93, Dolma.
[b]Gene designation according to Luthra and Chopra (1990).
[c]Bilara-2 and Fong Tien were susceptible to five PSH races and do not carry any known resistance gene(s). Therefore, Bilara-2 was used as standard susceptible check in all routine screening, both at seedling and adult-plant stages.

(Table 3). In this study, 49 (14.6%) of 336 genotypes showed adult-plant stage resistance in field screening (Table 4, Table S1). The summary of resistance reaction of barley genotypes to PSH races, a mixture of five known races Q, 24, 57, M and G under field conditions, is presented in Table 4. Overall, 50% of the genotypes showed either resistant (R) or moderately resistant (MR) infection responses while the remainder was susceptible to stripe rust. The seedling resistance indicated that 19%, 53.8%, 31.5%, 60.7% and 46.0% genotypes were resistant to races Q, 24, 57, M and G, respectively. The result of PCA using seedling resistance is presented in Figure 1. The vertices angles of each PSH races show that the PSH virulence in five races was diverse. Among five races, the vertex of PSH races 57 and M was most wide; therefore, these two races had different virulence than other races. The genotypes grouped in the same side of the PSH races showed higher susceptibility to that of PSH race. For example, PSH races G, 24, Q and 57 produced susceptible ITs on AM-21 and AM-245, but these genotypes were resistant to race M. Likewise, genotypes AM-92, AM-67 and AM-216 showed susceptible reaction to race M, but other races, G, 24, Q, and 57, produced resistance ITs on these genotypes. In contrast, genotypes away and opposite to the PSH vertices showed resistance responses. For example, genotypes AM-127, AM-276, AM-17, AM-236 and AM-319 showed resistance reactions to all PSH races in the seedling stage. The PCA of seedling and APR is shown in Figure S1. The high correlation of rust severity was found in Durgapur 2013 and 2014.

Twelve of 336 (3.6%) genotypes namely ARAMIR/COSSACK, Astrix, C8806, C9430, CLE202, Gold, Gull, Isaria, Lechtaler Piroline, Stirling and Trumpf were resistant to five PSH races evaluated at both seedling and the adult-plant stages (Table 5). In both seedling and APR screenings, Bilara-2 was highly susceptible to stripe rust confirming effectiveness of screening and sufficient inoculum pressure at all site-years. In Table 6, reaction of barley genotypes showing adult-plant stage resistance was presented. Of 336 barley genotypes screened for stripe resistance, 45 (13.4%) genotypes showed susceptible reaction to one of the races at the seedling stage but were resistant under the field conditions in 2013 and 2014 in both locations.

TABLE 3 Virulence//Avirulence formula based on responses of Indian differentials to *Puccinia striiformis* f. sp. *hordei* races (PSH) races originating from India

PSH races	Virulence//Avirulence[a]
57 (0S0)	*Rps4(Yr4)/rpsHF, rpsHi1/rpsHi2, rpsVa1/rpsVa2, rps1.c, rps1.b(yr), rps3(yr3)/rpsI5(Yr12,Yr13), rpsA14-1/RpsA14-2(yr1,yr10,yr11), Ukn*[b]*//**Ps1, rpsEM1/rpsEm2, Rps4/rpsAst, rps2(yr2), rpsTr1/rpsTr2, ps4, yrEB15561, ps4, yrEB1626-1, yrEB1626-2, yrEB1626-3 Ps1/ps4, Ukn*[c]
24 (0S0-1)	*Rps4(Yr4)/rpsHF, rpsEM1/rpsEm2, rps2(yr2), rps1.c, rps1.b(yr), rps3(yr3)/rpsI5(Yr12,Yr13), rpsA14-1/RpsA14-2(yr1,yr10,yr11), Ukn*[b]*//**Ps1, Rps4/rpsAst, rpsHi1/rpsHi2, rpsTr1/rpsTr2, ps4, yrEB15561, ps4, yrEB1626-1, yrEB1626-2, yrEB1626-3 Ps1/ps4, Ukn*[c]
G (4S0)	*rpsEM1/rpsEm2, rps1.c, rps3(yr3)/rpsI5 (Yr12,Yr13), rpsA14-1/RpsA14-2(yr1,yr10,yr11), Ukn*[b]*//**Ps1, Rps4 (Yr4)/rpsHF, Rps4/rpsAst, rpsHi1/rpsHi2, rpsVa1/rpsVa2, rps2(yr2), rpsTr1/rpsTr2, rps1.b(yr), ps4, yrEB15561, ps4, yrEB1626-1, yrEB1626-2, yrEB1626-3 Ps1/ps4, Ukn*[c]
M (1S0)	*Rps4(Yr4)/rpsHF, rpsEM1/rpsEm2, rpsVa1/rpsVa2, rps1.c, rps3(yr3)/rpsI5 (Yr12,Yr13) Ukn*[b]*//**Ps1, Rps4/rpsAst, rpsHi1/rpsHi2, rps2(yr2), rpsTr1/rpsTr2, rps1.b(yr), rpsA14-1/RpsA14-2 (yr1,yr10,yr11), ps4, yrEB15561, ps4, yrEB1626-1, yrEB1626-2, yrEB1626-3 Ps1/ps4, Ukn*[c]
Q (5S0)	*Rps4 (Yr4)/rpsHF, rps1.c, rps1.b(yr), rps3(yr3)/rpsI5(Yr12,Yr13), Ukn*[b]*//**Ps1, rpsEM1/rpsEm2, Rps4/rpsAst, rpsHi1/rpsHi2, rpsVa1/rpsVa2, rps2(yr2), rpsTr1/rpsTr2, rpsA14-1/RpsA14-2(yr1,yr10,yr11), ps4, yrEB15561, ps4, yrEB1626-1, yrEB1626-2, yrEB1626-3 Ps1/ps4, Ukn*[c]

[a]Virulence//avirulence formula is based on genes present in international and Indian differential lines used in this study., Stripe rust resistance genes upon which races are virulent are italicized. Stripe rust resistance genes upon which races are avirulent are boldface italicized. Genes separated by forward slice are present in same differential line while genes separated by a comma are present in different differential lines. Gene(s) in parenthesis are symbol used by Indian researchers.
[b]Unknown genes are mentioned as Ukn for susceptible infection responses of Bilara-2 and Fong Tien.
[c]Unknown genes are assigned as ***Ukn*** (boldface and italic) for resistance infection responses by Alfa93, and Dolma.

TABLE 4 Response of 336 barley genotypes to five races of *Puccinia striiformis* f. sp. *hordei* at seedling stage in glasshouse condition and at adult-plant stage resistance evaluated in field conditions under artificially controlled conditions in India

Infection Response[a]	Frequency of infection Responses	Seedling resistance[c]				
		57 (0S0)	24 (0S0–1)	G (4S0)	M (1S0)	Q (5S0)
R	49 (14.6)[b]	106 (31.5)	181 (53.8)	154 (46.0)	204 (60.7)	64 (19)
MR	119 (35.4)	–	–	–	–	–
MS–S	168 (50.0)	230 (68.5)	155 (46.2)	182 (54.0)	132 (39.3)	272 (81)

[a]MR, Moderately Resistant; MS, Moderately Susceptible; R, Resistant; S, Susceptible.
[b]Values in the parenthesis are percentage.
[c]*Puccinia striiformis* f. sp. *hordei* isolates used to evaluate barley genotypes.

4 | DISCUSSION

There are few stripe rust-resistant genes in barley reported effective against different PSH races in India (Bahl & Bakshi, 1963; Chen, Line, & Leung, 1998; Luthra & Chopra, 1990). In this study, we have reported the seedling and APR in 336 diverse barley genotypes with five predominant PSH races from India and found additional sources of PSH resistance in barley genotypes collected at ICARDA. Using international and Indian differential sets, we demonstrated the effectiveness of PSH resistance genes in Indian conditions. Given these results from both differential sets, race identification at seedling stage would be more effective and can explain the differences in the virulence present in the Indian races. Therefore, information on virulence/avirulence differences in PSH races against barley genes would help deployment and rotation of resistance genes in a farmers field in the future. Safavi, Jahani-Jelodar, and Ebrahimnejad (2015) reported that *rpsEm1*, *rpsEm2*, *rpsHF*, *Rps4*, *rpsVa1*, *rpsVa2* and *rpsAst* were effective while *rps2*, *Rps1.b*, *Rps3* and *rps I5* were not effective at all in

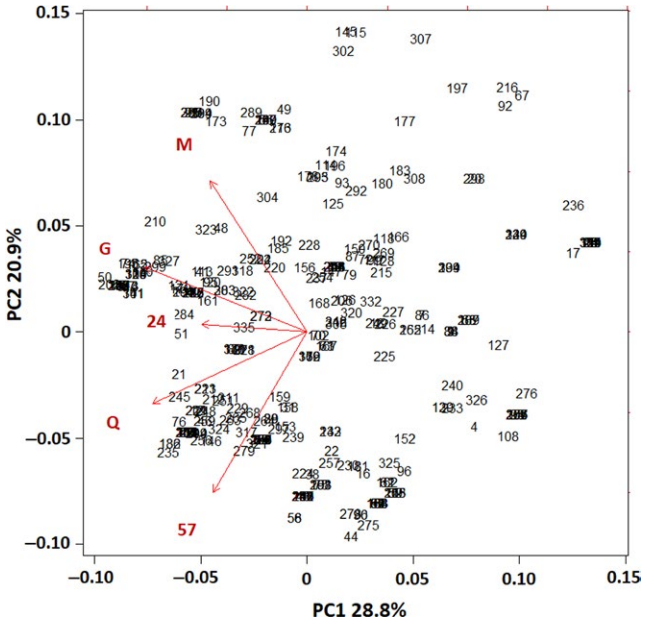

FIGURE 1 Principal component analysis of 336 barley genotypes for seedling resistance to the five *Puccinia striiformis* f. sp. *hordei* (PSH) races in India in 2015. The PSH races are boldface letters and numbers including 24, 57, G, M and Q

the field conditions in Iran. Our results show that several PSH resistance genes that were effective elsewhere were not effective in India. For example, genes *rps3* (*yr3*), *rpsl5* (*Yr12*, *Yr13*) possessed by I 5 were resistant to all races (PSH 1, 4, 10, 13, 20) (Chen et al., 1998) but were not effective for any of the five PSH races used in this study. Similarly, gene *rps1.c* that was effective against PSH 1, 4 and 10 in the USA (Chen et al., 1998) was ineffective to Indian PSH races tested here. These results indicate that virulences in PSH races prevalent in India are different than elsewhere in the world and need rigorous investigation before varietal development and gene(s) deployment. In contrast, *Rps4* (*Yr4*), *rpsAst* in Astrix and *rpsTr1*, *rpsTr2* in Trumpf were very effective against all five races tested in this study. It is worth noting that *Rsp4* was present in Heils Franken together with another recessive gene *rspHF* which were only effective to race G while other races (Q, 24, 57 and M) were virulent to both these genes. However, *Rsp4* present in Astrix with *rspAst* was very effective against all five races at seedling and adult-plant stages. Safavi et al. (2015) also reported that Astrix and Emir showed race-specific adult-stage resistance to PSH in Iran which is consistent with our study. Besides, *rspTr1*, *rspTr2* present in Trumpf was found highly resistant to all five races at seedling stage. *Ps1*, *ps4*, *yrEB15561*, *yrEB1626-1*, *yrEB1626-2*, and *yrEB1626-3* that are available in India (Luthra & Chopra, 1990) are still effective to all five PSH races at seedling stage. In this study, 12 additional sources of very high level of all stages (both seedling and adult-plant stages) resistance were found in genotypes ARAMIR/COSSACK, Astrix, C8806, C9430, CLE202, Gold, Gull, Isaria, Lechtaler, Piroline, Sterling and Trumpf. The results of this study indicate that these resistance sources are effective against PSH races in India and can furnish important resistance sources for future breeding programmes.

The PCA of ITs of PSH races on 336 barley genotypes was informative for barley researchers to select genotypes for crossing programme and to determine deployment of resistance genes based on PSH virulence. Specifically, selection of resistance genotypes, that were effective against all five PSH races, was easy with PCA biplot

TABLE 5 Genotypes showing all stage resistant reaction to *Puccinia striiformis* f. sp. *hordei* at seedling stage as well as adult-plant stage in two locations in India in 2013 and 2014

	Adult-plant stage reaction[a]			Overall	Infection type at seedling stage				
Genotype	DP-2013	DP-2014	KR-2014	Response[b]	57	24	G	M	Q
ARAMIR/COSSACK	0	0	0	[b]R	0	0	0	0	0
Astrix	0	0	0	R	0	0	0	0	0
C 8806	10R	0	0	R	0	0	0	0	0
C9430	0	0	0	R	2+	2+	0	0	0
CLE 202	0	0	0	R	0	0	0	0	0
Gold	15MR	15MR	0	MR	0	0	0	0	0
Gull	5MR	5MR	0	R	0	0	0	0	0
Isaria	0	0	0	R	0	0	0	0	0
Lechtaler	0	0	0	R	0	0	0	0	0
Piroline	0	0	0	R	0	0	0	0	0
Stirling	0	0	0	R	0	0	0	0	0
Trumpf	0	TMR	0	R	0	0	0	0	–
[c]Bilara-2	100S	100S	100S	S	3+	3+	3+	3+	3+

[a]DP, Durgapura, Rajasthan; and KR, Karnal, Haryana.
[b]Overall response was deduced from reactions in three field datasets, R, Resistant reaction; MR, Moderately resistant; TMR, Trace of moderately reaction infection response; S, Susceptible to PSH races 57 = (0S0), 24 = (0S0–1), G = (4S0), M = (1S0), and Q = (5S0).
[c]Bilara-2 was susceptible check.

TABLE 6 Adult-plant resistance of barley genotypes to five *Puccinia striiformis* f. sp. *hordei* (PSH) races under field and greenhouse conditions in India

Genotype	Durgapura 2013	Durgapura 2014	Karnal 2014	Overall[a] Response	Infection type[b] 57	24	G	M	Q
Haisa	0	0	0	R	0	0	0	0	3+
Ymer	0	TMR	0	R	3+	0	0	0	3+
Kenia	0	0	0	R	2+	0	0	0	3
MN 599	5R	5MR	0	R	3+	3+	0	0	3+
Quebracho	5MR	TMR	0	R	3+	3+	3+	0	3
ND10277	TMR	5MR	0	R	0	0	3+	3+	3
C 8828	15MR	TMR	0	R	0	0	0	0	3
CLE 257	5R	5R	0	R	3+	0	0	3+	0
C9430	0	0	0	R	2+	2+	0	0	0
C9609	0	5S	0	R	3+	3	0	3+	0
Moronera INIA	0	0	0	R	0	3+	0	0	0
BETZES	TR	5MR	10MR	R	3+	3	3	0	3+
MINAK	TR	0	0	R	3	3+	0	3+	3
LIGNEE640	0	0	0	R	2+	0	2	3	3
ROLAND-BAR	0	0	0	R	2–	0	0	3+	2+
GLORIA-BAR/COME	5MR	TMR	0	R	0	0	2+	3	3
83S.514	5R	5R	0	R	3	0	0	0	3+
CLN-B/80.5138//GLORIA-BAR/COPAL/3/LBIRAN/UNA80//LIGNEE640/4/MAMMUT/NOHA//GLORIA-BAR	TMR	5S	0	R	3+	0	3+	3+	3+
CAMPILLO LLERENA/DAPHNE//SEN	0	0	0	R	3+	0	0	0	3+
OROSUS	0	0	0	R	2+	0	2+	3+	3
MILAGROSA/CARDO//QUINA	0	5S	0	R	3	3+	3+	3+	3+
DUCO	0	5MS	0	R	0	0	3+	3+	3+
ALOE/GERANIO//MJA	0	0	0	R	3+	3+	3+	0	3+
TRIUMPH-BAR/TYRA//ARUPO*2/ABN-B/3/CANELA	TMR	0	0	R	3+	33+	3+	3+	3+
CARDO/VIRDEN/6/CEN-B/3/LBIRAN/UNA8271//GLORIA-BAR/COME/4/SEN/5/TOCTE	TMR	TMR	0	R	0	3	0	3+	3+
LBIRAN/UNA80//LIGNEE640/3/BBSC/4/CHAMICO	0	0	0	R	2+	3	3+	3+	3+
P.STO/3/LBIRAN/UNA80//LIGNEE640/4/BLLU/5/PETUNIA1	0	5S	0	R	3	3+	3+	0	3
PETUNIA 1/CALI92//BLLU	TMR	5S	0	R	0	0	3	0	3
TECOMA/MINN DESC 2//CIRU	0	5MS	0	R	0	0	–	3+	0
BELLA UNION	0	0	0	R	3	3+	3+	0	3+
CANELA	0	5MR	0	R	0	3+	3+	0	3+
MADRE SELVA	TMS	TMR	0	R	3	3+	3+	0	3+

(Continues)

TABLE 6 (Continued)

Genotype	Durgapura 2013	Durgapura 2014	Karnal 2014	Overall[a] Response	Infection type[b] 57	24	G	M	Q
PETUNIA 2	0	0	0	R	0	3+	0	0	3
ZIG ZIG	0	0	0	R	0	3+	3	0	3
CHAMICO/TOCTE// CONGONA	0	0	0	R	3	3	3	0	3
LIMON/BICHY2000	TMR	TMR	0	R	0	3+	0	0	0
ZIGZIG/BLLU//PETUNIA 1	5MR	0	0	R	0	0	3+	3+	3+
CANELA/CHERI	TMR	TMR	0	R	3+	0	0	0	0
LOGAN-BAR//FNC I 22/ DEFRA	TMR	0	0	R	0	0	3+	0	3
LA MOLINA 94	TMR	TMR	0	R	3	0	2+	3+	3+
LA MOLINA 96	TR	TMR	0	R	3+	0	3	3+	3
BEKA	0	0	0	R	3+	0	3	3+	3
HB120	TMR	5MS	0	R	3+	3	3+	3+	0
L94	0	0	0	R	3+	3+	3	3+	2+
Bancroft	0	0	0	R	3+	0	0	3+	0
Bilara-2	100S	100S	100S	S	3+	3+	3+	3+	3+

[a]R, Resistant; MR, Moderately Resistant; S, Susceptible to PSH races; TMR, Trace urediniospore with Moderately Resistant.
[b]PSH races used in the study: 57 = (0S0), 24 = (0S0–1), G = (4S0), M = (1S0), and Q = (5S0).

results. Genotypes AM-17, AM-236, AM-319, AM127, AM-154, AM-331, AM-64, AM-129, AM-169, AM-15, AM-2 and AM-23 were resistant to all five PSH races at seedling stages. Forty-five genotypes (13.4%) of 336 showed APR reaction in the field to the mixture of PSH races. Furthermore, the PCA of PSH resistance in barley genotypes (Figure S1) showed a high positive correlation of rust severity at Durgapura during 2013 and 2014 as indicated by the narrow vertex angles of rust severity in 2 years. There was a considerable positive correlation of rust severity in barley genotypes between Karnal-2014 and Durgapura in 2 years (2013 and 2014). In this study, we evaluated APR under field condition based on polycyclic infection by PSH races under artificial inoculation. Furthermore, APR was evaluated in multiple locations in multiple years in India. Hubbard and Bayles (2013) and Hovmøller (2007)suggested that the quantification of APR based on field screening under natural conditions and multiple assessments during rust development is most likely the accurate method for assessing APR in the host and adult-plant virulence of PSH races. The PCA of PSH resistance at seedling stage suggests PSH races used in this study have different virulences on barley genotypes (Figure 1) representing diverse PSH races prevalent in India. Specifically, M and 57 races were highly diverse relative to other races 24, Q and G. Considering the results from both the seedling and adult-stage screenings, we suggest that both all stage and adult-plant resistances, found in barley genotypes, are effective and accurate against PSH races in India. Further research is needed to confirm the APR reactions of these genotypes using individual races at adult-plant stage resistance to determine the APR to individual races.

Use of both seedling and APR is desirable for durability of rust resistance in cereals (Park, 2008). Furthermore, deployment of diverse gene(s) is desirable for the durability of resistance in barley breeding. These resistant genotypes possess additional and/or novel sources of resistance to stripe rust for both seedling and adult-plant stages; hence, these new resistant genotypes are valuable resources to diversify the contemporary resistance gene(s) in India. Twelve barley genotypes, namely ARAMIR/COSSACK, Astrix, C8806, C9430, CLE202, Gold, Gull, Isaria, Lechtaler Piroline, Stirling and Trumpf, were identified having resistance to PSH at seedling and adult-plant stages which could be excellent donor parents in developing resistant cultivars to PSH. However, the genetic makeup of these genotypes, except Astrix and Trumpf, is still unknown; therefore, further research is needed to understand the inheritance and allelism of PSH resistance genes in these genotypes. Based on their diverse geographical origin and parentage, we expect that these genotypes would provide additional sources of effective resistance against PSH at seedling as well as adult-plant stages. The comparison of both international and Indian differentials sets of PSH resistance has also revealed additional valuable resistance sources which are potential donor of resistance sources for the international community. The high level of APR identified in 45 genotypes provides additional protection against PSH in India. It will be therefore desirable to get these lines evaluated in other regions of the world to know the effectiveness of the resistance against different PSH races worldwide.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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SUPPORTING INFORMATION

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